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Rapid induced resistance and host species effects on gypsy moth, *Lymantria dispar* (L.): Implications for outbreaks on three tree species in the boreal forest

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Abstract

Field pupal weight, development time, and survival of gypsy moth, *Lymantria dispar* (L.), larvae on three defoliated (50%) and undefoliated tree species that are common to the forest of the Great Lakes basin were compared for one season in 1988. Host species and defoliation affected female pupal weight; male pupal weight was affected only by host species. The smallest and largest pupae of both sexes, from both defoliated and undefoliated trees, came from larvae that fed on red oak, *Quercus rubra* L., and trembling aspen, *Populus tremuloides* Michx., respectively; pupal weight of larvae that fed on white birch, *Betula papyrifera* Marsh., were intermediate. Development time was affected only by tree species; the shortest and longest development occurred on trembling aspen and red oak, respectively; development time on white birch was medial. Gypsy moth survival was not affected by defoliation or host species. Superficially, these data obviously suggest that both defoliated and undefoliated trembling aspen and white birch are more nutritious, and will support higher gypsy moth fitness than its traditional hosts like red oak. However, we argue that outbreaks of gypsy moth will not occur in aspen and birch stands because its tri-trophic fitness is lower there due in part to the higher efficacy of certain gypsy moth natural enemies. We hypothesize that outbreaks on these two tree species will be limited by the nuclear polyhedrosis virus, *Entomophagus maimaiga,* and key physical features (e.g. light trunk color) of the host that deter larval host-seeking/accepting behavior. More than 20 years of gypsy moth outbreak records in North America support this hypothesis.

Keywords: Gypsy moth; Rapid induced resistance; Defoliation; Induced plant defenses; Larval fitness

1. Introduction

Insect injuries often elicit complex physiological changes in plants that render them less suitable for future herbivory (Parry et al., 2003). Such changes have been described as rapid induced resistance (RIR) and delayed induced resistance (DIR) (Haukioja and Hanhimaki, 1985). It has been suggested that RIR may stabilize insect densities whereas DIR may contribute to population cycles (Haukioja et al., 1988; Haukioja, 1990). However, some studies have reported negligible induced plant defenses (Fowler and Lawton, 1985), or even induced amelioration, i.e. improved insect growth and survival after herbivory (Niemela et al., 1984; Haukioja et al., 1990).

Many studies have investigated the relationship between gypsy moth, *Lymantria dispar* (L.), defoliation and host plant quality (Wallner and Walton, 1979; Schultz and Baldwin, 1982; Valentine et al., 1983; Rossiter et al., 1988; Barbosa et al., 1990a,b). Without exception, they have established that tree species common to the forest of New England, such as red oak, *Quercus rubra* L., produce defensive plant chemicals that can adversely affect larval development. However, less is known about defoliation-induced defenses against the gypsy moth in trembling aspen, *Populus tremuloides* Michx., and paper birch, *Betula papyrifera* Marsh., two very abundant trees in the Great Lakes basin (Osier and Lindroth, 2001; Parry et al., 2003). Witter et al. (1990) and Roden and Surgeoner (1991) have reported that trembling aspen is a highly favorable host, producing faster growth, and more fecund adults than red oak. However, the outbreak potential in the vast boreal and sub-boreal forests of trembling aspen and paper birch is open to

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speculation. Consequently, it is important to not only identify the nutritional value but also the defensive response of potential gypsy moth host plants in the Great Lakes basin. In this study we test whether there is evidence for RIR in trembling aspen, paper birch, and red oak by measuring fecundity, development time and survival and then compare our observations and conclusions to gypsy moth development and outbreaks in the Great Lakes basin during the subsequent 19 years.

2. Materials and methods

2.1. Study area and insects

In 1986 we selected a 2-ha site situated 10 km northeast of Arden, Ontario (44°43′N, 76°56′W) based on descriptions of forest sites where gypsy moth would be expected to do well (Houston and Valentine, 1977; Houston, 1979). The site consisted of saplings that had re-established on abandoned farmland. Trees were inspected in 1986 and 1987 to insure that they had not been defoliated and were not infested with other herbivores. In 1988, prior to beginning the experiment, forest tent caterpillar, *Malacosoma disstria* Hbn., eggs were found on several trees. All of these were removed by hand. Subsequently, the base of each tree was coated with Stikem Special® (Seabright Enterprises, 4026 Harlan St., Emeryville, CA) to prevent ancillary miscellaneous inter-tree herbivore movement during the experiment. Study trees were widely dispersed throughout the stand; the mean diameter (measured at dbh) and height were 5.51 ± 0.18 cm and 5.9 ± 0.08 m, respectively. All trees had full exposure to the sun to minimize the effect of shade on leaf quality (Larsson et al., 1986; Mole et al., 1988).

We used larvae from gypsy moth egg masses that were collected randomly on 10 April 1988 at the edge of a new infestation at Kaladar, Ontario (44°39′N, 77°07′W). Eggs were surface-sterilized (Shapiro, 1977) and then held at +5 °C until incubation so that larval emergence could be synchronized with gypsy moth emergence in the field. After eclosion, larvae were then reared on artificial diet (Bell et al., 1981) in the laboratory until second instar before being transferred to trees in the field.

2.2. Experimental design

We employed a randomized complete block design with a two by three factorial arrangement of treatments with sub-samples to test for RIR by measuring gypsy moth survival, pupal weight, and development time to pupation. There were two levels of defoliation (factor 1) (0 and 50%) crossed by three tree species (factor 2), trembling aspen, paper birch, and red oak. The six treatment combinations were replicated four times (blocks), each replication done on consecutive days because it was not possible to install more than six treatments per day. The tree was the experimental unit, where we established 20 larvae, 5 on each of 4 terminal branches (sub-samples), enclosed by a 50 cm × 30 cm nylon mesh bag. During the larval feeding period, which lasted from 26 May to 17 July, the feeding bags were moved to new terminal shoots weekly to insure that larvae never consumed more than 50% of the available foliage. Shoots that were used as feeding sites were marked with flagging tape and were not used again. The bags reduced light transmission (measured by a light meter) by about 15%. The placement of larvae on the trees was synchronized with second-instar larval development in the field. The replication (block) dates were: 26, 27, 28, and 30 May. To reduce experimental variation, we chose defoliated and undefoliated trees of each species within replications to be as similar as possible, and we used mean initial second-instar larval fresh weight per tree (on the day larvae were installed) as a covariate. Pupae, morphologically sexed, were weighed fresh within 24 h of pupation.

2.3. Simulated defoliation

We simulated gypsy moth defoliation by tearing leaves by hand (parallel to the leaf mid-rid) throughout the canopy of each tree on three occasions (6–9, 15, and 22 June). For the first two simulated levels of defoliations, every 10th leaf was torn in half (5% cumulative defoliation for each defoliation); this coincided with damage in the field that occurred when the majority of larvae reached third and fourth instar. For the final date, every remaining undefoliated leaf was torn (50% cumulative defoliation) coincident with the inception of fifth- and sixth-instar larval development in the field. The tearing of foliage for the first defoliation was completed at the rate of one replication per day; for the last two defoliation levels, all replications were completed the same day. Tukey's HSD test ($\alpha = 0.05$) was used for separation of the means for gypsy moth pupal weight and development time. All data from the experiment were analyzed with SAS GLM. We did not analyze any replication by treatment interactions because we did not originally plan for this. It would have required a large increase in the number of replicates in order to rigorously address these potential effects. Hence all such interaction variation is imbedded in the error term.

3. Results

3.1. Defoliation effects

Current year defoliation treatments significantly ($p < 0.01$) reduced female but not male pupal weights (Table 1). Averaged over tree species, defoliation reduced female growth by about 12%, after adjusting for small differences in initial weights of second instars (Table 2). There were no significant defoliation × tree species (D × TS) effects (Table 1), so that defoliation consistently induced lower weights of female pupae on all three trees. On the other hand, defoliation had no significant effect on development time (Table 3), or on survival rates (Table 4). Furthermore, because there was no significant D × TS interactions for either pupal mass, development time, or survival, this means that all tree species responded similarly to the defoliation treatment as measured from the insect's perspective.

Table 1
Analysis of variance of gypsy moth pupal weights, as influenced by defoliation and tree species

Source	Female			Male		
	df	MSE	*F*	df	MSE	*F*
Total corrected	35			63		
Replication	3	0.072	3.58*	3	0.044	7.45**
Defoliation	1	0.186	9.91**	1	0.004	0.78
Tree species	2	0.826	41.16***	2	0.059	10.04**
Defoliation × tree species	2	0.040	2.01	2	0.002	0.43
Covariate (mean L_2 weight/cage)	1	0.148	7.37*	1	0.038	6.46*
Experimental error (variance between trees)	9	0.020	0.77	14	0.005	2.18*
Sampling error (variance between cages)	17	0.026		40	0.002	

* Significant at $\alpha = 0.05$.
** Significant at $\alpha = 0.01$.
*** Significant at $\alpha = 0.001$.

3.2. Tree species effects

As expected, tree species had a substantial significant effect on both female and male pupal masses, with the pattern as follows: aspen > birch ≥ red oak. When averaged over defoliation, male and female pupal weights on aspen were about 25 and 70% larger, respectively, than those on oak (Table 2). The pattern for gypsy moth development times was exactly the reverse, i.e. days to develop on red oak ≥ birch > aspen. Larvae on red oak required about 4 days more to develop than those on aspen (Table 2). Survival did not differ among tree species. Furthermore, there was no evidence of a significant D × TS interaction.

3.3. Replicate and covariate effect

Surprisingly, there was a significant starting date or replicate effect on both pupal mass and development time (Tables 1 and 3). We did not expect this because each succeeding replicate was only 1 day later than its predecessor, meaning that the first and last replicates were only 4 days apart and implies that small differences in establishment date may have profound effects on larval development and success, perhaps due to rapid phenological changes in plant development (Lawrence et al., 1997). Another noticeable aspect of the ANOVA is the significant covariate effect for initial second-instar larval weight for both female and male pupal weights (Table 1). Although we did not know it when we installed larvae on trees,

Table 3
Analysis of variance of gypsy moth development time, as influenced by defoliation and tree species

Source	Female			Male		
	df	MSE	*F*	df	MSE	*F*
Total corrected	35			63		
Replication	3	126.11	14.24**	3	84.27	11.81**
Defoliation	1	20.30	2.29	1	4.68	0.66
Tree species	2	40.10	4.53*	2	47.08	6.60**
Defoliation × tree species	2	8.83	1.0	2	0.30	0.04
Covariate (mean L_2 weight/cage)	1	2.30	0.26	1	20.33	2.85
Experimental error (variance between trees)	9	8.86	2.07	14	7.13	1.84
Sampling error (variance between cages)	17	4.27		40	3.87	

* Significant at $\alpha = 0.05$.
** Significant at $\alpha = 0.01$.

Table 4
Analysis of variance of gypsy moth pupal survival, as influenced by defoliation and tree species

Source	Female			Male		
	df	MSE	*F*	df	MSE	*F*
Total corrected	35			63		
Replication	3	0.747	0.77	3	0.684	0.43
Defoliation	1	0.012	0.01	1	0.459	0.29
Tree species	2	0.970	1.00	2	0.585	0.37
Defoliation × tree species	2	0.761	0.79	2	1.319	0.83
Covariate (mean L_2 weight/cage)	1	1.724	1.78	1	0.001	0.00
Experimental error (variance between trees)	9	0.969	1.45	14	1.584	1.37
Sampling error (variance between cages)	17	0.669		40	1.153	

No results were significant at $\alpha = 0.05$.

Table 2
Mean pupal fresh weights (g) and development times (days) for gypsy moth larvae reared from second instars until pupation on control and defoliated aspen, birch, and red oak saplings

Defoliation treatment	Aspen		Birch		Red Oak		Grand means[a]	
	Male	Female	Male	Female	Male	Female	Male	Female
Pupal mass (g)								
Control	0.49	1.48	0.40	1.17	0.41	0.89	0.43 a	1.11 b
Defoliation	0.49	1.32	0.40	1.01	0.36	0.68	0.42 a	0.99 c
Grand means[b]	0.49 a	1.43 d	0.40 b	1.13 e	0.39 b	0.84 f		
Development time (days)								
Control	41.0	43.7	44.4	48.4	44.0	49.8	43.3 a	48.0 a
Defoliation	40.7	52.0	42.6	48.4	43.9	52.2	42.4 a	50.3 a
Grand means[b]	40.8 a	46.1 d	43.6 b	48.4 d, e	44.0 b	50.4 e		

[a] Grand means of the same sex followed by different letter are significantly different ($p < 0.05$); values averaged over host species.
[b] Grand means of the same sex followed by different letters are significantly different ($p < 0.05$) according to Tukey's HSD test; values averaged over defoliation treatment.

Table 5
Source of mortality and number of larvae surviving from second instar to adult eclosion for female and male gypsy moth larvae reared on defoliated and undefoliated host species

Treatment	*n*	Deaths from		Survivors	
		NPV[a]	*P. placidus*	Female	Male
Undefoliated trees	240	0	141	27	62
Defoliated trees	240	2	134	29	70

Larval deaths from *E. miamaga* not observed in the stand at the time of the experiment.
[a] Nuclear polyhedrosis virus.

there was enough variation in the sizes of second instars to cause trees to differ in their initial cohort body masses which translated into differences in their pupal masses.

3.4. Mortality

Gypsy moth mortality, observed bi-weekly, was unaffected by either defoliation or tree species; however, there is a real possibility it may have been masked by late fifth- and sixth-instar larval mortality that resulted from attacks by *Podisus placidus* Uhl. (Pentatomidae). This predator voraciously attacked larvae through the nylon screening as they crawled on the interior surface of the bag. However, because all treatments used to evaluate survival were insignificant (Table 4) we conclude that mortality in the experiment, although high because of this predator, was randomly distributed between treatments and hence did not affect pupal weight and development time measurements for survivors. Furthermore, the number of larvae that escaped from cages in the experiment or that died as a result of nuclear polyhedrosis virus (NPV) or other diseases was negligible (Table 5). *Entomophagus maimaiga* (Entomophthoraceae) was not detected at the time of the experiment.

4. Discussion

The study plainly suggests that significant defoliation contemporaneous with gypsy moth feeding in later instars can elicit depressed growth of female gypsy larvae on three common tree species, each in a different family, i.e. Salicaceae, Betulaceae, and Fagaceae. Females, but not males, responded to defoliation treatments, we hypothesize, because male growth was nearing completion when the final and most severe defoliation treatment was applied. Females take about 5–7 days longer to finish development than males and hence were exposed longer to the defoliation-induced effects. While we cannot prove that the reduction in gypsy moth growth was truly due to RIR, rather than some concomitant purely nutritional effect, we do know that tearing leaves in half as was done in this experiment, triggers substantial increases in aspen total phenolics, and tannins, but not changes in leaf N (Mattson and Palmer, 1988; Osier and Lindroth, 2001). Many studies clearly show that the general nutritional quality of food for gypsy moth declines after severe defoliation (Wallner and Walton, 1979; Schultz and Baldwin, 1982; Rossiter et al., 1988; Osier and Lindroth, 2001; Parry et al., 2003). All three tree species used in the present study are hosts that are characterized by a leaf chemistry comprised mostly of phenolics (Barbosa and Krischik, 1987), which have been shown to vary inversely with gypsy moth pupal weight and fecundity (Rossiter et al., 1988; Hemming and Lindroth, 1995; Hwang and Lindroth, 1997; Parry et al., 2003).

The time required for larval development in our study was not affected by the slight-moderate defoliation treatment; however, host species strongly influenced development time (Table 3). Larvae consistently developed slower on red oak than on trembling aspen and paper birch (Table 2). These results concur with those of Wallner and Walton (1979) who found that defoliation of oak prolonged larval development compared to that on grey birch.

Close correspondence of our study's pupal weights with those of Wallner and Walton (1979), and Maksimovic (1958), and development times on trembling aspen similar with those reported by Witter et al. (1990); and Roden and Surgeoner (1991), and the fact that gypsy moth development on oak does not always yield the most fecund pupae (Barbosa, 1978; Lance and Barbosa, 1982) impart confidence to our findings and their general applicability in the field. It is especially noteworthy, however, that all studies of gypsy moth development on trembling aspen share one particular finding: pupal weights of larvae fed on trembling aspen, a host not traditionally associated with outbreaks of gypsy moth, are significantly heavier than those of larvae that fed on red oak, a traditionally highly ranked host of *L. dispar*. Because gypsy moth development on trembling aspen produced potentially more fecund pupae in a shorter development time than larvae reared on red oak, a pressing question is whether the abundant pure stands of trembling aspen, paper birch or both, will (or can) support volatile outbreaks of gypsy moth in the forests of the upper Great Lakes and boreal North America.

In an earlier report Roden (1992) hypothesized that pure stands of trembling aspen and white birch would not support populations of gypsy moth unless there was a strong component of oak present. He suggested there were several reasons for this. First, survivorship, development and reproductive success of an insect depend obviously, in part, on its ability to select appropriate sources of nutrition. Consequently, an insect's host preference is often closely correlated with the most nutritionally suitable host in its environment (Tabashnik, 1986). Nevertheless, mismatches between host preference and nutritional suitability can and do occur because the insect is compelled to survive in a tri-trophic niche (Singer and Stireman, 2005). For example, poor correspondence between host preference and nutritional suitability has been attributed to other important ecological factors such as competitors, and natural enemies (Smiley, 1978; Price et al., 1980) which can make even the most nutritious host inappropriate, or host finding and acceptance behavior that is not directly related to host nutritional suitability because such suitable habitats are avoided (Singer, 1971; Chew, 1981; Singer and Stireman, 2005). We suggest that the generally poor correspondence between gypsy moth outbreaks and hosts that have been

identified as more nutritious in this study and others (Roden and Surgeoner, 1991; Witter et al., 1990) exist because gypsy moth fitness is restricted on these hosts due to the high effectiveness of NPV and certain unique physical features of the host that negatively affect larval behavior and development.

Secondly, although Witter et al. (1990) reported outbreaks of gypsy moth in stands of trembling aspen, these were either in mixed stands of aspen with oak or were merely ephemeral infestations which support our contention. The historical, long standing absences of gypsy moth outbreaks in stands of trembling aspen in Maine, where infestations should probably have occurred by now because of the state's long standing exposure to gypsy moth, and more recently in Ontario, further support our contention. For these reasons, we believe that the success of gypsy moth in the Great Lakes basin will be much restricted in stands dominated by a high trembling aspen and paper birch basal area, not only because of the demonstrated effectiveness of NPV on such hosts, but also because larvae are highly attracted to tree trunks of darker color, larger diameter and height (Roden et al., 1992) which is stronger than its attraction to a preferred foliage (Smitley et al., 1993). In mixed forests, where species other than oak are present, larvae will be attracted after first-instar dispersal to species with darker trunks (Roden et al., 1992), such as maple (*Acer*) and ash (*Fraxinus*) which are suboptimal for development (Hough and Pimentel, 1978; Lance and Barbosa, 1982; Roden and Surgeoner, 1991). In mixed forests that contain a low oak basal area, gypsy moth populations may minimally subsist, but as the basal area of aspen and birch increases in the stand, population growth will be restricted by a combination of NPV and the increasingly high incidence of *E. maimaiga* which appears to infest most stands (Nealis et al., 1999) in the Great Lakes basin today.

Although there have been sporadic outbreaks in stands of trembling aspen and white birch in Ontario (Canadian Forest Service Forest Insect and Disease Reports, 1985–2003), these have been minor, i.e. confined to extremely small areas for short periods on exceptionally poor sites. Consequently, for the reasons we outlined, we argue that large stands of trembling aspen and white birch will not be severely infested as more than 20 years of historical data reveal.

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